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A reassessment of the Cretaceous amber deposits from France and their palaeontological significance

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ABSTRACT

The Cretaceous amber deposits from France are reviewed, and their palaeontological content is discussed in the light of recent studies. Numerous "old" amber localities mentioned at the beginning of the 20th century or studied during the 1970s are no longer accessible, but recent field investigations have led to the discovery of new deposits. Among these, the Late Albian amber from Charente-Maritime (SW France) is particularly rich in biological inclusions and thus constitutes one of the major fossiliferous amber deposits for the Cretaceous period. Without having all groups studied, the authors made significant new records and identified taxa occuring in this French amber. This contributes to an improvement of our current knowledge on the evolution and diversity of Mesozoic insects.

KEY WORDS: Amber, Cretaceous, France, arthropods, insects, assemblages, inclusions.

INTRODUCTION

Studies of the Cretaceous amber of France started at the beginning of the 20th century when Lacroix (1910) described the physical and chemical properties of what he named "retinites", and listed approximately fifty deposits of Cretaceous fossil resins. Among these, he cited the presence of an abundant yellow opaque resin in the Cenomanian lignitic clay from two north-western regions (Sarthe and Maine-et-Loire) and from Enet Island (Charente-Maritime, SW France) (Fig. 1). He considered this latter locality as the most important French deposit of fossil resin, together with that of Saint-Lon in Landes (Fig. 1). From various sites Lacroix collected numerous samples which were deposited in the Muséum national d'Histoire Naturelle (MNHN) in Paris. Further chemical analyses were launched between 1963 and 1978, mainly on Cretaceous resins from Sarthe and Charente-Maritime (Chauffin 1963; Schlüter 1978; Savkevitch & Popkova 1978). Based on infrared spectroscopy, the latter placed these resins close to valchovite, a Russian variety of fossil resin (Savkevitch 1974). Some amber pieces collected by Schlüter, but of unknown provenance (probably Bezonnais in Sarthe, Lambert, pers. comm.), were later used for a Nuclear Magnetic Resonance characterisation of Cretaceous amber (Lambert *et al.* 1996; Lambert & Poinar 2002) and were ranged within the group of *Agathis*-like resins.

Galippe (1920) first studied the micro-organisms of amber from Briollay (Maine-et-Loire), but detailed examinations for fossiliferous content were attempted only in the 1970s with Cenomanian ambers from north-western France. Indeed, Kühne *et al.* (1973) described a micropterygid lepidopteran from Bezonnais, and Schlüter (1978) recorded Ascomycetes and 71 fossil arthropods, mainly insects, from Bezonnais and Durtal. He described or figured 34 species in 13 insect families and 5 specimens in Arachnida (Table 1). He also analysed some amber pieces from the Lower Cenomanian of the

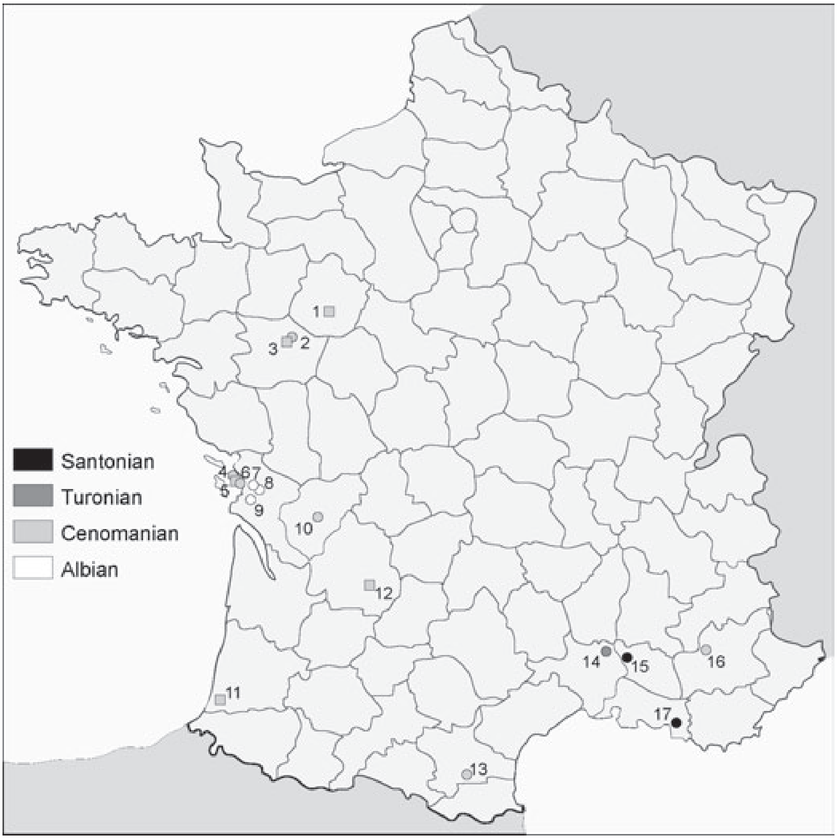

Fig. 1. Geographical location and age of the Cretaceous amber deposits of France. Squares correspond to localities previously studied but no longer available in 2005, circles mark the outcrops which are currently visible: (1) Ecommoy (Bezonnais); (2) Durtal; (3) Briollay; (4) Aix Island; (5, 6) Fouras Peninsula: (5) Enet Island, (6) Fouras/Bois-Vert; (7) Tonnay-Charente (Les Renardières); (8) Archingeay-Les Nouillers; (9) Cadeuil; (10) Champniers (La Buzinie); (11) St-Lon; (12) St-Cyprien; (13) Fourtou; (14) St-Marcel-de-Carreiret; (15) Piolenc; (16) Salignac; (17) Belcodène.

Fouras Peninsula and Aix Island in Charente-Maritime, but without any discovery of fossil inclusions. Later, Matile (1981), Schlüter and Stürmer (1982), Schlüter (1983, 1989) and then Szadziewski and Schlüter (1992) gave further details and new descriptions for this entomofauna (Table 1).

Waggoner (1994) described an aquatic micro-assemblage of bacteria, fungi and protists from the Cenomanian amber of Bretagnolles (Eure). However, this provenance seems to be erroneous and the amber is likely to have originated from Bezonnais where similar micro-organisms were recently described (Breton & Tostain 2005).

Thus, previous studies of the French Cretaceous amber focused mainly on the Cenomanian deposits of Bezonnais and Durtal (NW France), and almost all studies were based on chemical analyses, which established an araucarian origin for the amber. Curiously, studies of the fossiliferous content were rather scarce, and less than one hundred inclusions were recorded in 12 arthropod orders.

TABLE 1

List of inclusions previously mentioned from the Cretaceous (Cenomanian) amber of France.

Group	Family	Taxon	Provenance
Arachnida			
Opilionida		sp. A [b]	Bezonnais
Acari		sp. A, B [b]	-
Araneae		sp. A, B [b]	-
Insecta			
Blattodea		sp. A [b]	-
Isoptera		*Lutetiatermes prisca* [a]	-
		Mastotermes sarthensis [a]	-
		sp. C, D, E, F, G [b]	-
Psocoptera		sp. A [b]	-
Heteroptera		sp. A [b]	-
Neuroptera	Rhachiberothidae	*Retinoberotha stuermeri* [b]	-
Coleoptera	Staphylinidae	*Stenus inexpectatus* [b]	-
		Staphylininae sp. A [b]	-
Lepidoptera	Micropterygidae	sp. A [c]	Durtal
Hymenoptera	Mymaridae	*Galloromma bezonnaisensis* [b]	Bezonnais
	Scelionidae	*Cenomanoscelio pulcher* [b]	-
		sp. A, B, C [b]	-
	Sphecidae	*Gallosphex cretaceus* [b]	-
	Diapriidae	Ismarinae indet. [b]	-
	Falsiformicidae	sp. A [b]	-
	Fam. indet.	sp. A, B, C [b]	-
Diptera	Empididae	*Ecommocydromia difficilis* [b]	-
	Limoniidae	sp. A [b]	-
	Ceratopogonidae	*Atriculicoides cenomanensis* [d]	Durtal
		Atriculicoides incompletus [d]	-
		Austroconops borkenti [d]	Bezonnais
		Leptoconops [d]	-
	Cecidomyiidae	sp. A [b]	Durtal
	Keroplatidae	*Schlueterimyia cenomanica* [e]	Bezonnais
	Nematocera indet.	sp. A [b]	-

TOTAL, described or figured arthropods: 39; TOTAL, mentioned inclusions: 71

[a] Schlüter 1989; [b] Schlüter 1978; [c] Kühne *et al.* 1973; [d] Szadziewski & Schlüter 1992; [e] Matile 1981.

MATERIAL

In a general conspectus of all the French ambers, Nel *et al.* (2004*a*) mentioned 55 Cretaceous localities (12 Albian, 32 Cenomanian, 2 Turonian, 3 Santonian, and 6 Maastrichtian). This included some newly discovered localities as well as those previously listed in the literature (Lacroix 1910; Schlüter 1978), but lacked any detail with regard to their present availability. Here we present the state of the art in our investigations launched since 1999 in order to recover the 'historical' localities as well as to discover new deposits. Twelve outcrops are currently available for excavation of amber (Fig. 1), among which ten are fossiliferous. Their ages and a list of their biological content are presented and discussed below. The preliminary analyses of three of them, previously presented by Néraudeau *et al.* (2002, 2003, 2005) and Perrichot (2004), are also completed. Material from the "old" localities studied by Schlüter is held in the Institut für Paläontologie, Museum für Naturkunde, Berlin, Germany. The material from all other studies is held in the Laboratoire de Paléontologie, Muséum national d'Histoire Naturelle, Paris, France. The discussion below only deals with personal data on the latter material, data on faunal assemblages from "old" localities being used for comparison in the conclusion section.

RESULTS

The rich amber-bearing Cenomanian strata of Bezonnais and Durtal (NW France, Sarthe and Maine-et-Loire) were located in quarries which do not exist today. However, an old quarry still exists close to Durtal (e.g., Briollay), which provided a few amber fragments without any inclusions. We failed to find new available outcrop in these regions. Investigations into the mid-Cretaceous amber of northern France have also failed, although Albian and Cenomanian strata containing numerous fragments of lignitic wood are still exposed on the cliffs of the Seine-Maritime region. Lastly, we were unable to locate the presumably rich (Lacroix 1910) amber-bearing deposits of Enet Island and St-Lon (Aquitain basin), as well as those mentioned around St-Cyprien in the Sarladais (Lacroix 1910; Colin 1973), due to the current bad condition of the outcrops.

In south-eastern France, five deposits currently yield a small amount of amber. Cenomanian deposits at Fourtou and Salignac (Fig. 1: localities 13 and 16) provide dark red-coloured nodules ranging from 5 to 30 mm and representing fragmented flows, in which about 30 and 15 arthropods have been found respectively (Table 2). In the three other deposits of Turonian and Santonian age (Fig. 1: localities 14, 15 and 17), most of the amber pieces are translucent light yellow to red-coloured marbles ranging from 3 to 10 mm in diameter. From these, fossil insects have been detected only in the Santonian amber of Piolenc and Belcodène (Table 2).

Finally, six amber deposits of both Albian and Cenomanian age have been accessible in Charente-Maritime and Charente departments in the last five years (Fig. 1: localities 4, 6–10), including those of Fouras Peninsula and Aix Island which were previously studied by Schlüter (1978). Analyses have revealed biological inclusions in all of the six amber deposits, although only the locality of Archingeay-Les Nouillers is highly fossiliferous (Table 2). Indeed, this is the most fossiliferous amber deposit thus far for the Cretaceous of France and the second richest among all French ambers after that of the Eocene of Oise (Nel *et al.* 2004*a*). The five other deposits have provided fewer inclusions since they were either discovered more recently and need further analyses (quarry of Cadeuil and trench of motorway works in La Buzinie at Champniers), or the outcrops are less or no longer accessible in 2005 and thus provided a smaller amount of material (Fouras Peninsula and Aix Island cliffs, and quarry of Les Renardières at Tonnay-Charente). Amber from the six localities presents similar properties and is thought to be mainly of araucarian origin, although other conifers of the families Cheirolepidiaceae and Podocarpaceae might also have contributed to the resin production (Perrichot 2004, 2005).

DISCUSSION

Without having all amber pieces examined, nearly 900 biological inclusions are recorded so far from ten newly reported fossiliferous Cretaceous deposits, with about 760 inclusions from the Late Albian amber of Archingeay-Les Nouillers (Table 2). This fossil assemblage is mainly composed of insects but also contains other arthropods such as Arachnida, Crustacea and Myriapoda (Fig. 2A), vertebrate remains such as a reptile skin (Perrichot & Néraudeau 2005) and several feathers, plant remains (wood) and various micro-organisms (bacteria, fungi, algae, diatoms, dinoflagellates, etc.). Micro-inclusions are not considered here because studies of these organisms have only just started. For arthropods, numerous taxa are still not identified beyond the order or family level and require further analyses. However, significant new records and taxa already occur.

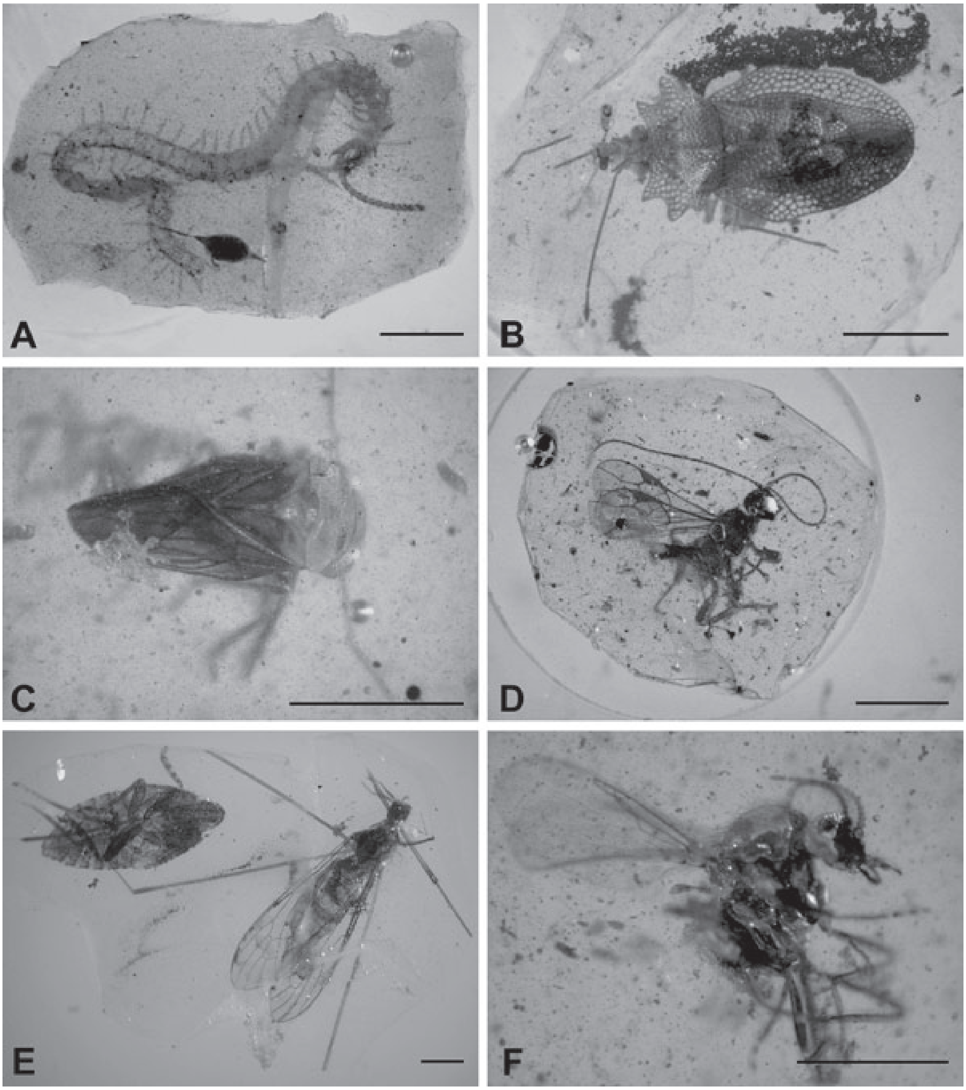

Fig. 2. Various arthropod inclusions in the Late Albian amber of SW France: (A) Chilopoda, MNHN Buz 1.8, La Buzinie; (B) Heteroptera Tingidae, MNHN Cdl 2.28, Cadeuil; (C) Heteroptera Schizopteridae, MNHN Buz 1.5, La Buzinie; (D) Hymenoptera Braconidae, Protorhyssalinae, MNHN Cdl 2.30, Cadeuil; (E) Diptera Limoniidae and Hemiptera Achilidae, MNHN Arc 186.2, Archingeay-Les Nouillers; (F) Diptera Ceratopogonidae, MNHN Cdl 2.1, Cadeuil. Scale bars = 1 mm.

Arachnida

Arachnids form about 9% of total arthropod inclusions in the Albian amber of France, while they are nearly absent from the Cenomanian amber. Two Pseudoscorpionida and a Scorpiones of the extinct family Palaeoeuscorpiidae (Lourenço 2003) are recorded, but most are Acari and Araneae.

TABLE 2

List of inclusions newly reported from the Cretaceous amber of France.

Group	Taxon	
ARCHINGEAY– Late Albian		
Kingdom Plantae		
Conifera (wood)	Araucariaceae [#]	many
Kingdom Animalia		
Phylum Vertebrata		
Reptilia (skin)	indet. [#]	1[a]
feathers	indet.	7
Phylum Arthropoda		
Isopoda	indet.	11
Tanaidacea	indet.	1
Diplopoda	Polyxenida indet.	1
Myriapoda	indet. [#]	1
Pseudoscorpionida	Cheliferidae	2
Scorpionida	Palaeoeuscorpiidae [#]	1[b]
Acari	indet.	39
Araneae	Zodariidae	3
	indet.	23
	TOTAL	26
Collembola	indet.	11
Strepsiptera	indet.	6
Blattodea	Umenocoleidae	1
	indet.	29
Dermaptera	indet.	5
Isoptera	indet. [#]	2
Orthoptera	Gryllotalpidae	2[c]
	Grylloidea	7
	Tridactylidae	6
	Acridoidea?	2
	indet.	14
	TOTAL	31
Sternorrhyncha	Coccoidea	7
Auchenorrhyncha	Achilidae	4
	Fulgoroidea	9
	TOTAL	13
Heteroptera	Gerridae	2[d]
	Gerromorpha indet.	1[d]
	Schizopteridae	2[e]
	Tingoidea	2[f]
	indet.	5
	TOTAL	12
Hemiptera	indet.	4
Psocoptera	Trogiomorpha	8[g]
	indet.	18
	TOTAL	26
Thysanoptera	Thripidae?	1
	indet.	1
	TOTAL	2
Raphidioptera	Mesoraphidiidae? [8]	1
Neuroptera	Ascalaphidae [8]	1
	Myrmeleontidae[8]	3
	Rhachiberothidae	1[h]
	Coniopterygidae	1[i]
	indet.	1
	TOTAL	7
ARCHINGEAY (*continued*)		
Coleoptera	Buprestidae	1
	Curculionoidea	1
	Elateridae	1
	Ripiphoridae	2[j]
	Scraptiidae	1
	Staphylinioidea	2
	indet. [#]	25
	TOTAL	33
Lepidoptera	indet.	5
Hymenoptera	Ceraphronoidea	3[k,l]
	Chalcidoidea	31
	Cynipoidea	3
	Diapriidae	1[l]
	Formicidae	14[m]
	Ibaliidae?	1
	Ichneumonidae? [#]	2
	Proctotrupoidea	1
	Scelionidae	11[l]
	Siricidae?	1
	Sphecidae?	1
	Trigonalidae	1[n]
	indet.	28
	TOTAL	98
Diptera	Bombyliidae? [#]	1
	Cecidomyiidae	1
	Ceratopogonidae	35
	Chironomidae	8
	Dolichopodidae	45[o]
	Hilarimorphidae?	1
	Limoniidae	3[p]
	Mycetophiloidea	1
	Phoridae	2
	Psychodidae	18[q]
	Rhagionidae	4
	Tipuloidea indet. [#]	8
	Brachycera indet. [#]	105
	Nematocera indet. [#]	43
	indet. [#]	45
	TOTAL	320
Insecta	indet. [#]	65
	TOTAL, inclusions	760
CADEUIL – Late Albian		
Acari	indet.	3
Blattodea	indet.	2
Auchenorrhyncha	Fulgoroidea	1
Heteroptera	Tingidae	1
Psocoptera	indet.	1
Thysanoptera	indet.	1
Coleoptera	indet. [#]	1
Lepidoptera	indet.	1
Hymenoptera	Braconidae	2[l]
	Ceraphronoidea	2[l]

Group	Taxon	
CADEUIL (continued)		
Hymenoptera	Chalcidoidea	2
	Megalyridae	1[l]
	Scelionidae	4[l]
	Scolebythidae	1[l]
	indet.	5
	Total	17
Diptera	Ceratopogonidae	4
	Chironomidae	2
	Dolichopodidae	3
	Psychodidae	1
	Nematocera indet. [#]	1
	Brachycera indet. [#]	5
	Total	15
	TOTAL, inclusions	44
LES RENARDIÈRES – Late Albian		
Diptera	Nematocera indet. [#]	2
LA BUZINIE – Early Cenomanian		
Kingdom Plantae		
Conifera (leaf)	indet.	1
Kingdom Animalia		
Tanaidaceae	indet.	2
Chilopoda	indet.	1
Acari	indet.	1
Collembola	indet.	1
Blattodea	indet.	1
Heteroptera	Schizopteridae	2[e]
Diptera	Dolichopodidae	9
	TOTAL, inclusions	17
FOURAS – Early Cenomanian		
Araneae	indet. [#]	1
Acari	indet.	3
Coleoptera	Nitidulidae	1
Sternorrhyncha	Aleyrodidae	1
Hymenoptera	Formicidae	2[m]
	Scelionidae	5[l]
	indet.	1
	Total	8
Diptera	Ceratopogonidae	4
	Dolichopodidae	1
	Phoridae?	1
	Brachycera indet. [#]	1
	Nematocera indet. [#]	2
	Total	9
Insecta	indet.	2
	TOTAL, inclusions	25
AIX ISLAND – Early Cenomanian		
Trichoptera	indet.	1
Diptera	indet. [#]	1
Hymenoptera	Formicidae?	1
	TOTAL, inclusions	3

Group	Taxon	
FOURTOU – Early Cenomanian		
Tanaidacea	indet.	6
Hemiptera	indet.	1
Hymenoptera	Scelionidae	1[l]
	Stigmaphronidae	1
	indet.	3
	Total	5
Diptera	indet.	17
	TOTAL, inclusions	29
SALIGNAC – Cenomanian		
Diplopoda	Synxenidae	1[r]
Heteroptera	Tingoidea	1[f]
Coleoptera	Ripiphoridae	1[j]
Diptera	indet.	12
	TOTAL, inclusions	15
PIOLENC – Santonian		
Hymenoptera	indet.	6
Diptera	indet.	9
	TOTAL, inclusions	15
BELCODENE – Santonian		
Diptera	indet.	1[#]
TOTAL, Cretaceous amber of France		911

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[8] Larvae; [#] fragments; [a] Perrichot & Néraudeau 2005; [b] Lourenço 2003; [c] Perrichot *et al.* 2002; [d] Perrichot *et al.* 2005; [e] Perrichot *et al*. in press; [f] Perrichot *et al*. 2006; [g] Perrichot *et al.* 2003; [h] Nel *et al.* 2005*b*; [i] Nel *et al.* 2005*a*; [j] Perrichot *et al.* 2004*a*; [k] fam. incertae sedis, Perrichot *et al.* 2004*b*; [l] Perrichot *et al.* in prep.; [m] Perrichot *et al.* submitted; [n] Nel *et al.* 2003; [o] Nel *et al.* 2004*c*; [p] Perrichot *et al.* 2007; [q] Azar *et al.* 2003; [r] Nguyen Duy-Jacquemin & Azar 2004.

Within spiders, three specimens have been identified as members of the family Zodariidae. They show the unusual reduction of spinnerets characteristic of the family. The arrangement of eyes and the positioning of the legs give them a systematic position close to the subfamily Zodariinae. Interestingly, modern Zodariinae are specialised predators feeding exclusively on ants (Pekár & Křál 2002). Thus, the presence of zodariids together with that of several ants in the same deposit suggests that such a predator-prey relationship could have existed since the Early Cretaceous at least. Other fossil Zodariidae are extremely scarce, being mentioned in Eocene Baltic amber only (Wunderlich 1995).

So far, the Cretaceous family Lagonomegopidae is not reported from French amber. This is somewhat surprising, considering its presence in ambers from Siberia, New Jersey, Canada, Myanmar and Spain (Eskov & Wunderlich 1994; Penney 2002, 2004, 2005, 2006). Among the major fossiliferous Cretaceous amber deposits, Lagonomegopidae are absent only from Lebanon and France.

Heteroptera

Gerromorpha: Mesozoic gerromorphan or semi-aquatic bugs are rather scarce, although Andersen (1998) estimated a Jurassic divergence of most of the eight extant families. The only fossils known thus far are four Cretaceous records: two representatives of the family Hydrometridae from the Aptian Santana Formation of Brazil and from the Albian Burmese amber (Nel & Popov 2000; Andersen & Grimaldi 2001), and Veliidae and Mesoveliidae from the Aptian of the Koonwarra fossil beds in Australia (Jell & Duncan 1986). The oldest known fossil Gerridae, a sister family of the Veliidae, and one Gerromorpha of undetermined family are recorded in the Albian amber of Archingeay-Les Nouillers. A description and discussion is provided elsewhere (Perrichot *et al.* 2005*a*).

Cimicomorpha: Tingoidea are represented by the family Tingidae in the Albian amber of Cadeuil (Fig. 2B), and by a family *incertae sedis*, similar to Vianaididae, in the Albian and Cenomanian amber of Archingeay-Les Nouillers and Salignac. The Tingidae would be the only Mesozoic and the oldest known representative of the family as Nel, Waller and De Ploëg (2004) considered the two Lower Cretaceous genera *Golmonia* and *Sinaldocalder* (Popov 1989) as Heteroptera *incertae familiae*. So far, 38 fossil species of Tingidae have been described, all of Cainozoic age (Wappler 2003; Nel, Waller & De Ploëg 2004).

According to Schuh and Slater (1995), the Gerromorpha is the sister group of the Panheteroptera (=Nepomorpha + Leptopodomorpha + Pentatomorpha + Cimicomorpha). The finding of new representatives of both the Cimicomorpha and Gerromorpha in the Albian and Cenomanian French amber is thus of considerable significance for the phylogeny and chronology of the "higher" Heteroptera (=Panheteroptera).

Dipsocoromorpha: This is one of the most primitive groups within the true bugs (Heteroptera). Four specimens of the family Schizopteridae, or jumping ground bugs, are recorded from the Late Albian amber of Archingeay-Les Nouillers and the Early Cenomanian amber of La Buzinie at Champniers (Fig. 2C). They represent a new genus very similar to the extant *Hypselosoma*, suggesting great morphological stability of this small bug family whose fossil record is very sparse. Cainozoic specimens are recorded from the Oligocene–Miocene Dominican and Mexican ambers, and from the

Eocene Baltic amber. Mesozoic fossils are mentioned from the Albian Burmese and Neocomian Lebanese ambers (Poinar 1992; Popov & Herczek 1993; Grimaldi *et al.* 2002), but none of these fossils has been described thus far. The Schizopteridae and Tingoidea are described and discussed elsewhere (Perrichot *et al*. 2006, in press).

We hypothesise that the Dipsocoromorpha: Enicocephalidae could also occur in the French Cretaceous amber, as this is a sister group of the Schizopteridae (according to Schuh & Slater 1995) and because several representatives have been found in the Lebanese and Burmese ambers (Azar *et al.* 1999; Grimaldi *et al.* 2002).

Coleoptera

Compared with other Cretaceous ambers, Coleoptera are rather infrequent in both the Albian and Cenomanian deposits, comprising about 4% and 1% of the total arthropod inclusions respectively. The oldest Ripiphoridae are recorded as two distinct genera: the extinct *Paleoripiphorus* from the Albian amber of Archingeay-Les Nouillers and the extant genus *Macrosiagon* from the Cenomanian amber of Salignac (Perrichot *et al.* 2004*a*). Grimaldi *et al.* (2002) reported, but did not describe, the only other known Cretaceous specimen, from Burmese amber, and rare ripiphorids are reported from the Eocene Baltic amber and the Palaeogene of Florissant (Kaup *et al.* 2001; Meyer 2003). Other beetles assigned to Buprestidae, Elateridae, Nitidulidae, Scraptiidae, Staphylinidae and Curculionoidea also occur, but the specimens have yet to be studied.

Neuroptera + Raphidioptera (Neuropterida)

These are quite uncommon with only eight specimens from Archingeay-Les Nouillers, almost all being larvae. Six specimens belong to the neuropteran families Ascalaphidae, Myrmeleontidae, Rhachiberothidae (Nel *et al.* 2005*b*) and Coniopterygidae. Within the latter, the specimen is the oldest representative of the extant tribe Fontenelleini of the subfamily Aleuropteryginae (Nel *et al.* 2005*a*). One raphidiopteran specimen is represented by the head capsule of a larva. The distinct collar visible in all extant raphidiopteran larvae (Aspöck 1998) is absent here, as in the two other Cretaceous snakefly larvae previously described with two adult forms from the Burmese and New Jersey ambers (Grimaldi 2000; Engel 2002). Thus, the larval specimen probably belongs to the same extinct family Mesoraphidiidae. Among Cretaceous ambers, it is the fourth larva and the sixth specimen for this family, the only other specimen being an undescribed head of a larva from Lebanon. This specimen gives further evidence of the past distribution of snakeflies in tropical habitats, whereas today they are restricted to temperate regions of the Northern Hemisphere (Aspöck 1998).

Hymenoptera

Hymenoptera is the second largest group, after Diptera, in terms of the number of specimens (14% and 11% for the Albian and Cenomanian ambers respectively), but the largest in terms of diversity, with 12 families recognised and at least three others still undetermined. This hymenopteran fossil assemblage is somewhat distinct, both in present groupings and relative abundance, compared to other fossiliferous Cretaceous ambers.

Symphytans are exceptionally rare in amber: Orussidae have been described only from New Jersey (Basibuyuk *et al.* 2000) and Siberia (Rasnitsyn 1977). In Spain, another specimen of this family and one Anaxyelidae have been found, but are not yet described

(Martínez-Delclòs *et al.* 1999). The amber from Archingeay-Les Nouillers contains a putative Siricidae, but further preparation of the inclusion is needed for an accurate systematic attribution due to the very cloudy aspect of the amber piece.

All other Hymenoptera discovered in the French ambers are apocritans, and Parasitica make up 85% of the total hymenopteran specimens belonging to at least 12 families: Trigonalidae, Megalyridae, Stigmaphronidae, Scelionidae, Diapriidae, Ibaliidae, Braconidae, Ichneumonidae and yet undetermined families of the Ceraphronoidea, Proctotrupoidea, Chalcidoidea and Cynipoidea. Aculeata belong to the families Scolebythidae, Sphecidae and Formicidae. Chalcidoidea dominate in this assemblage but are not yet studied at the family level. Scelionidae is the most abundant family with 24% of all specimens collected, represented by four distinct genera and five species. It is not surprising that they are common and diverse, as in all Cretaceous ambers, as this group appeared during the Early Cretaceous and diversified extensively during the mid-Cretaceous (Rasnitsyn 2002). More surprisingly, Formicidae is the second largest family, representing 12% of all hymenopteran specimens.

The Trigonalidae is the oldest described fossil representative of this family (Nel *et al.* 2003), but several specimens are recorded in the Aptian amber of Álava, Spain (Martínez-Delclòs *et al.* 1999). Within Diapriidae, the oldest representative of Belytinae is recorded, with previous accurate records not being mentioned before the Eocene. Two specimens found in the Albian amber of Cadeuil belong to the Protorhyssalinae (Fig. 2D) and are the second and oldest occurrence of this extinct braconid subfamily, which was previously described only from the Turonian amber of New Jersey (Basibuyuk *et al.* 1999). Lastly, five ants are recorded in at least three distinct genera: a putative worker of uncertain subfamily in the extinct genus *Gerontoformica* (Nel *et al.* 2004*b*), an alate female and an incomplete worker closely resembling the extinct Burmese amber genus *Haidomyrmex* Dlussky, 1996, and two sphecomyrmine workers of the extinct Burmese amber genus *Sphecomyrmodes* Engel & Grimaldi, 2005 (Perrichot *et al.* submitted-*b*). In addition, 11 inclusions are putatively attributed to the Formicidae, but they are preserved in opaque amber and need further analysis for accurate identification. So far, they are the oldest known ants together with those from the contemporaneous Burmese amber. Descriptions and further discussions of all these apocritans, with the exception of Ibaliidae, Sphecidae, Stigmaphronidae, Proctotrupoidea, Chalcidoidea and Cynipoidea, are provided elsewhere (Nel *et al.* 2003, 2004*b*; Perrichot *et al.* 2004*b*, in prep.).

Diptera

Diptera is the most abundant group of inclusions in both the Albian and Cenomanian ambers of France (43% and 23% respectively), as in all fossiliferous resins. Similarly, Dolichopodidae, Ceratopogonidae, Psychodidae and Chironomidae dominate (nearly 37% and 74% of all dipteran inclusions for Albian and Cenomanian respectively). Detailed analysis is needed in order to evaluate the diversity in each family.

Within dolichopodids, a new species of the microphorine genus *Microphorites* is common and largely dominant (Nel *et al.* 2004*c*), but at least two other undetermined genera also occur. *Microphorites* was previously described from the Lebanese amber (Hennig 1971; Grimaldi & Cumming 1999) and mentioned in Burmese and Spanish ambers (Grimaldi *et al.* 2002). The psychodids are almost exclusively represented by a new species of *Eophlebotomus*, an extinct genus occurring in the Lebanese and Burmese ambers (Cockerell 1920; Duckhouse 2000; Azar *et al.* 2003). In addition, two distinct genera have been found in the Albian amber of Archingeay-Les Nouillers and Cadeuil, belonging to the subfamily Sicoracinae or Trichomyinae. Finally, Tipuloidea are rather common inclusions in amber from Archingeay-Les Nouillers. Almost all are incomplete and represented by wings or legs only, but three Limoniidae of the genus-group *Limonia* are preserved (Fig. 2E; Perrichot *et al.* 2007). This is the oldest record of the genus *sensu lato*, which is frequently found fossilised in the Tertiary of Europe (Evenhuis 1994) but rather infrequently in the Cretaceous, being described only from the Turonian amber of New Jersey (Gelhaus & Johnson 1996) and the Campanian amber of Canada (Krzemiński & Teskey 1987).

Ceratopogonidae or biting midges are common and abundant (Fig. 2F) as in all Cretaceous ambers. Szadziewski and Schlüter (1992) described three genera in the Cenomanian amber of NW France: *Atriculicoides*, *Leptoconops* and *Austroconops*. Thus, we predict that these genera may occur in the Albian and Cenomanian amber presented herein. Other genera such as *Minyohelea*, *Protoculicoides* and *Archiaustroconops* could also be expected, due to their occurrence in ambers from Lebanon, Myanmar or Spain (Szadziewski 1996, 2004; Szadziewski & Arillo 1998; Borkent 2000) where dipteran assemblages show common taxa (e.g., *Microphorites*, *Eophlebotomus*).

CONCLUSION

With 26 arthropod orders and numerous other biological inclusions recorded in eight Albian and Cenomanian amber deposits, the present analysis of newly recovered material demonstrates that the palaeontological significance of the mid-Cretaceous amber of France was hitherto underestimated. Actually, this amber, together with ambers from Lebanon, Spain, Myanmar, New Jersey, Canada and Siberia, rates as one of the seven major fossiliferous Cretaceous ambers.

During the mid-Cretaceous, the Charente-Maritime region was composed of a mosaic of coastal habitats with peculiar plant associations, from littoral to lacustrine environments and intermediate mangrove-like areas, under a warm and wet subtropical climate but with probable arid seasons (Moreau 1993; Néraudeau *et al.* 2002, 2003, 2005; Perrichot 2004, 2005; Gomez *et al.* 2004; Videt 2004; Dejax & Masure 2005). The amber-producing forest, mainly composed of Araucariaceae, Podocarpaceae and Cheirolepidiaceae (Perrichot 2005), was probably located in this mangrove-like environment. Indeed, there is evidence that the resin could have flowed directly into brackish water: diatoms, dinoflagellates and cyanobacteria characteristic of this type of environment have been found as micro-inclusions in many amber pieces (Breton & Tostain 2005), and typically marine arthropods are also included within the fossilised assemblage (e.g., Crustacea Tanaidacea and Heteroptera Gerridae). The rest of the arthropod assemblage is consistent with such an environment, with numerous representatives of the ground habitat of humid forests preserved in the "litter amber" (Perrichot 2004). The important number and variety of predators and parasites suggest a high diversity for the biocenosis of the original ecosystem.

Schlüter (1978) and Breton and Tostain (2005) proposed a similar palaeoenvironmental reconstruction for the Cenomanian deposits of NW France. Despite these similarities, some differences occur in the taxonomic diversity observed between amber from the two regions: some groups described by Schlüter (1978) in the amber of NW France are absent from the amber of SW France (e.g., Hymenoptera: Mymaridae and Falsiformicidae, Diptera: Keroplatidae), and when a family is found in both ambers, subordinate taxa are different (e.g., Neuroptera: Rhachiberothidae, Hymenoptera: Diapriidae). So far, only the Cenomanian amber of Fourtou (Corbières) has yielded a scelionid wasp similar to that of the amber from Bezonnais, NW France (e.g., *Cenomanoscelio pulcher*). Full appreciation of the diversity of the French Cretaceous ambers will require further detailed studies.

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